FEEDING STRUCTURES, BEHAVIOR, AND MICROHABITAT OF *ECHINOCYAMUS PUSILLUS* (ECHINOIDEA: CLYPEASTEROIDA)

MALCOLM TELFORD, ANTONY S. HAROLD, AND RICH MOOI

Department of Zoology, University of Toronto, Ontario, Canada, M5S 1A1

ABSTRACT

In the Firth of Lorne, Scotland, *Echinocyamus pusillus* was found most abundantly in highly variable, poorly sorted substrates at depths of 10–20 m. It was common in areas exposed to extensive wave and tidal current activity, but absent in fine sediments in sheltered areas. In size, feeding mechanism, and behavior, the species is highly adapted for nestling in the interstices between relatively large pebbles. The feeding mechanism is atypical for clypeasteroids: substrate particles with attached organisms are selected and transported by the suckered podia. At the mouth, particles are held in place and slowly rotated by the free margin of the peristomial membrane, while the teeth strip away diatoms and organic debris. The peristomial membrane and ciliation of spines and podia are shown in scanning electron micrographs of critical point dried material. The histology of these structures is described with special reference to mucus secretion. High resolution SEM micrographs show mucus secreting pores among the epithelial microvilli of suckered and buccal podia but not in the epithelium of miliary spines. The suggestion that *E. pusillus* might represent a sand dollar ancestor is discussed. The evidence presented supports the view that it is specialized rather than primitive.

INTRODUCTION

The fibulariids are a family of very small clypeasteroids including two principal living genera, *Fibularia* and *Echinocyamus*. These genera have most often been regarded as specialized rather than primitive forms (Clark, 1914; Mortensen, 1948). The family is thought to be most closely related to the Laganidae and Rotulidae (Mortensen, 1948; Hyman, 1955; Durham and Melville, 1957, *inter alia*). That species of *Echinocyamus* are specialized has not been accepted universally. Cuénot (1941) considered *E. pusillus* to be clearly primitive and proposed that the family Fibulariidae was the evolutionary point of departure leading to the more advanced clypeasteroids. Phelan (1977) seems to support this interpretation as does the phylogenetic dendrogram shown by Durham and Melville (1957). Most recently Ghiold (1982), following a study of such external structures as spines, podia, and pedicellariae, concluded that *E. pusillus* was not a true sand dollar and suggested that it and similar forms " . . . may represent an ancestral stage of the sand dollars."

The fundamental body forms of the Clypeasteroida appear to be shaped by hydrodynamic forces (Telford, 1981; Telford and Harold, 1982; and Telford, in press) and by the requirements of their peculiar rocking-sieve feeding mechanism (Goodbody, 1960; Seilacher, 1979; Mooi and Telford, 1982). In assessing the status of *Echinocyamus,* correct interpretation of morphology depends in part on understanding the chosen habitat and the feeding mechanism. Neither Nichols (1959), in the most extensive study of the morphology of *Echinocyamus,* nor Ghiold (1982) were able

to make direct observations of feeding. Therefore, previous knowledge of this process has been based only on inference. The species has been reported in "shelly gravel" (Nichols, 1959). Ghiold (1982) made a laboratory study of burrowing and locomotory activity in different sized sediment particles, but no complete sieve analyses of natural substrates have been given. Wolff (1968) reported that *E. pusillus* was abundant in the North Sea in "relatively coarse sands," with a median grain size of 210–460 μm. No further details of substrate composition were provided.

We present an account of the feeding mechanism of *E. pusillus* from direct laboratory observations. Additional morphological details of the structures involved, based on scanning electron microscopy (SEM) and histological examination, are provided. Substrate analysis, SEM examination of natural substrate material and analysis of gut contents are also presented in an attempt to explain local distribution, within the Firth of Lorne, Scotland.

Materials and Methods

Collection

Specimens of *Echinocyamus pusillus* were collected by dredge with 91.4 cm × 30.5 cm rectangular mouth, fitted with a double layer of 6 mm string mesh, inside a protective heavy rope mesh and by Petersen grab, 36.8 × 33.0 cm. Animals were washed from the substrate by gently swirling with water in a plastic bowl, the method was analogous to gold panning but in this case we retained the lightweight urchins. Specimens were either fixed immediately or returned live to the laboratory where they were maintained in natural substrate material washed by constant running sea water at approximately 4°C.

Live observations

To observe feeding, the methods of Mooi and Telford (1982) were used. Animals were placed in darkened glass chambers constructed from microscope slides. They were given a thin layer of natural substrate with the larger particles (>4.0 mm) removed. Observations were made using a stereomicroscope focussed on an inclined front-silvered mirror beneath the chamber. Illumination was provided by a fiber optic light. Substrate particles handled by feeding animals were measured *in situ* by ocular micrometer. Gut contents of fresh animals were examined under the light microscope and those of preserved animals by SEM.

Specimen preparation

All material used in this study was fixed for 12 hours in 2% gluteraldehyde in filtered sea water. Specimens were then briefly rinsed and stored in 2% formalin in filtered sea water. Relaxation was difficult but best results were obtained by gradually transfering specimens to 3.5% Epsom salts in distilled water. Suckered podia were also well relaxed by propylene phenoxytol-saturated sea water. For histology, specimens were decalcified in Bouin's solution for 24 to 48 h (Mooi and Telford, 1982). Paraffin sections were cut at 4 μm and stained with Milligan's trichrome and Mallory-Heidenhain rapid one-step azan for general histology. Toluidine blue and PAS were used to investigate secretory structures. All histological procedures followed the methods of Humason (1967). For SEM, whole or dissected specimens were transferred through a graded series to pure acetone, critical point dried with carbon dioxide in a SORVALL bomb, and sputter coated with gold in a SEM-PREP II (Nannotech Thin Films,

England). Substrate particles and gut contents were gently washed in distilled water to remove salts, strewn on stubs, and freeze-dried before sputter coating.

Substrate

Samples were taken from the grab and dredged material. They were dried at 80°C, weighed, and then ashed at 400°C for 30 min. After cooling and reweighing, the samples were passed through screens of mesh size 12.50, 4.00, 2.00, 1.00, 0.50, and 0.25 mm, into a collecting pan. Each fraction was weighed separately and expressed as a percentage of the total. Organic content, calculated from weight lost during ashing, was similarly expressed as a percentage of the total dry weight. Repeated ashing confirmed that organic material was fully oxidized in the initial 30 minute period. Estimates of shell (biogenic) to mineral (abiogenic) particle ratios were made by frequency from light microscope observation. Whenever possible, the generic origin of the biogenic material was noted.

RESULTS

Habitat

Echinocyamus pusillus (4–14 mm length) was collected at several sites in the Firth of Lorne (Fig. 1), at depths of 10 to 200 m. They were most abundant in shallow water, 10–20 m, and very sparse below about 50 m. We found no *E. pusillus* living in sheltered areas such as Loch Creran nor in the lee of islands but they tended to be common in locations which, according to the West Coast of Scotland Pilot (1949),
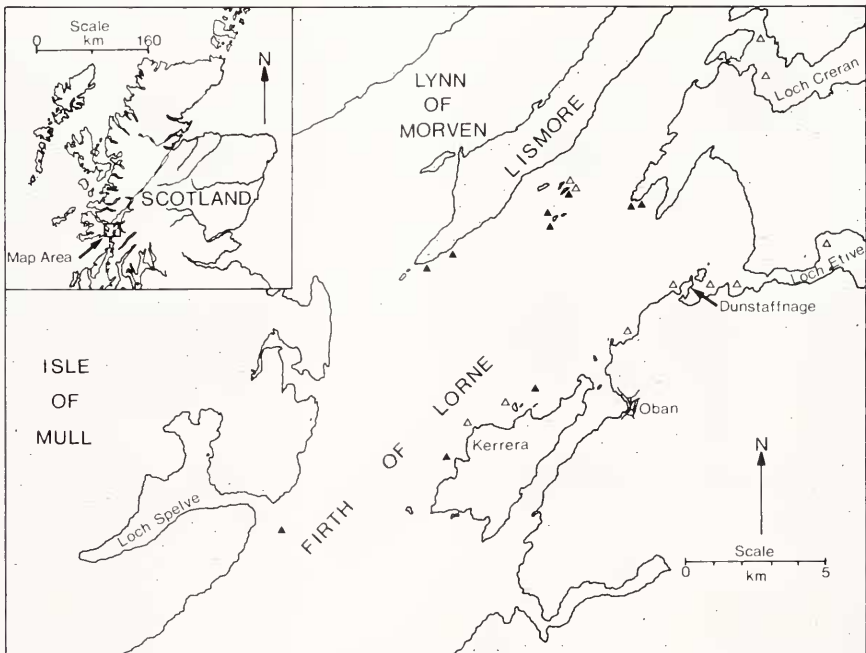

FIGURE 1.   Collection sites in the Firth of Lorne, West Scotland. Solid symbols mark locations where *Echinocyamus pusillus* was obtained by dredging; open symbols indicate absence.

are exposed to strong currents. Greatest numbers (over 100 in a 10 minute dredge haul) were obtained along the exposed side of a promontory on the north side of a small bay, Camas Nathais (56°29'N, 05°28'W). Six of seven grab samples taken from this site contained live *E. pusillus*. Analysis of particle sizes showed the substrate to be poorly sorted and highly variable (Table I). The Petersen grab tends to bias samples towards the smaller particle fractions, failing to collect the larger pebbles or rocks, sometimes returning to the surface empty. Several samples from the same location, were taken separately from the dredged material, from which unknown amounts of the finer particles had been lost during collection. A comparison of these with the grab material is shown in Table I. The fraction >12.5 mm included pebbles up to 100 mm, rarely to 200 mm. Bigger pebbles, often with attached macrophytic algae, were not included. Estimates of the ratio of shell to mineral particles, in different fractions of the samples, showed considerable variability (Table II). However, the shell component tended to be greatest around the 0.50 mm fraction. Maximum numbers of animals were found when the shell:mineral ratio in this size range was between 2:1 and 10:1, that is, about 67% to 91% shell material. Identification of organisms contributing to the shell component was possible in the larger particle fractions (Table II). Above 0.5 mm the shell comes primarily from the locally dominant pelecypods and gastropods. Below 0.5 mm, echinoderm spines and forams make significant contributions. Organic contents of the substrate were likewise rather variable, ranging from 0.8% to 2.7% by dry weight. We did not detect any correlation between organic content and the proportion of biogenic substrate particles. Substrate samples collected from several other sites in the Firth of Lorne and their characteristics were also very variable (Table III). *Echinocyamus pusillus* was not found in muddy substrates, with high proportions of fine particles (<0.25 mm).

General behavior

E. pusillus occupies the spaces between relatively large pebbles (>12.5 mm) where it either nestles (Nichols, 1959) or burrows (Ghiold, 1982) in pockets of sandy gravel. Substrate particles were moved over both the oral and aboral surfaces of exposed animals, by the action of suckered podia. Once covered, individuals retained a complete canopy of particles held firmly against the spine tips by the suckered podia, even when they were fully buried. The animals retracted their podia and gradually released particles when disturbed. During hours of daylight *E. pusillus* moved about very little but during darkness they often relocated themselves. Between the spines, water currents flow towards the peristome and from there to the periproct, as described previously (Nichols, 1959). These currents are generated by bands of cilia along the shafts of miliary spines, placed at right angles to the current flow (Fig. 2F); additional cilia are

TABLE I

Comparison of substrate samples taken by Petersen grab (n = 7) and dredge (n = 9) from the shallow bay, Camas Nathais (marked by two triangular symbols in Fig. 1)

Source	>12.5 mm	>4.0 mm	>2.0 mm	>1.0 mm	>0.5 mm	>0.25 mm	<0.25 mm
Grab	13.1	10.5	11.3	19.7	17.8	13.9	13.7
	±18.2	±10.3	±6.9	±11.9	±10.4	±10.3	±9.8
Dredge	12.0	13.7	18.5	25.7	16.2	9.8	4.6
	±9.1	±5.9	±6.6	±5.0	±4.6	±4.9	±2.8

Mean particle fractions (±S.D.) expressed as percent dry weight.

TABLE II

Shell to mineral particle ratios by number, expressed as percentages, and origin of biogenic material for substrate samples in which Echinocyamus pusillus *was abundant*

Dredge substrate samples:

Fraction	4.0 mm	2.0 mm	1.0 mm	0.5 mm	0.25 mm
Range	15–90	30–85	50–90	30–95	25–95
Median	55	70	70	75	60

Petersen grab samples:

Range	5–80	2–75	1–80	1–90	10–85
Median	20	55	60	75	70
Origin	Pelecypoda Gastropoda Polychaeta Echinodermata	Pelecypoda Gastropoda Echinodermata	Pelecypoda Gastropoda Echinodermata	Echinodermata Foraminifera	Foraminifera Echinodermata

Pelecypoda: *Astarte, Venerupis, Chlamys, Ensis, Cardium.*
Gastropoda: *Turritella, Patella, Calliostoma.*
Echinodermata: *Echinus, Psammechinus, Echinocyamus, Echinocardium.*
Median values for shell material give a good indication of the "typical" substrate.

located in relatively shorter bands on the primary spines, where they are restricted to the spine bases (Fig. 2B).

Feeding

During feeding, substrate particles were picked up and initially transported by the suckered podia which actively explored the substrate. Under the experimental conditions it was not possible to see whether podia on the aboral surface contributed equally to this process. Particles were held by the combined action of the sucker and secreted mucus: occasionally particles adhered to podia even when their suckers were fully expanded and visible. The handled particles ranged from 0.25 to 1 mm but were mostly about 0.5 mm in maximum dimension. The animals manipulated biogenic

TABLE III

Particle size fractions as percent dry weight for dredged substrate samples in which Echinocyamus pusillus *was abundant, present, or absent*

	>12.55 mm	>4.0 mm	>2.0 mm	>1.0 mm	>0.5 mm	>0.25 mm	<0.25 mm
Abundant	52.5	44.6	2.5	0.3	0.1	0.1	0.1
	13.0	21.6	29.9	26.3	8.6	0.4	0.3
	47.7	41.7	8.6	1.3	0.4	0.2	0.2
	27.2	61.5	2.0	1.9	5.8	1.4	0.2
Present	73.5	8.9	3.2	3.4	6.1	2.9	1.8
	49.2	25.3	17.6	6.0	1.1	0.5	0.4
	17.8	23.2	25.8	21.7	9.2	1.9	0.5
Absent	44.7	22.9	1.5	2.7	3.9	4.2	20.2
	53.2	8.3	4.0	5.5	7.5	7.1	14.2
	0.0	6.6	0.5	1.9	1.6	2.7	85.9

Results from single dredge hauls; samples too variable to justify calculation of means.
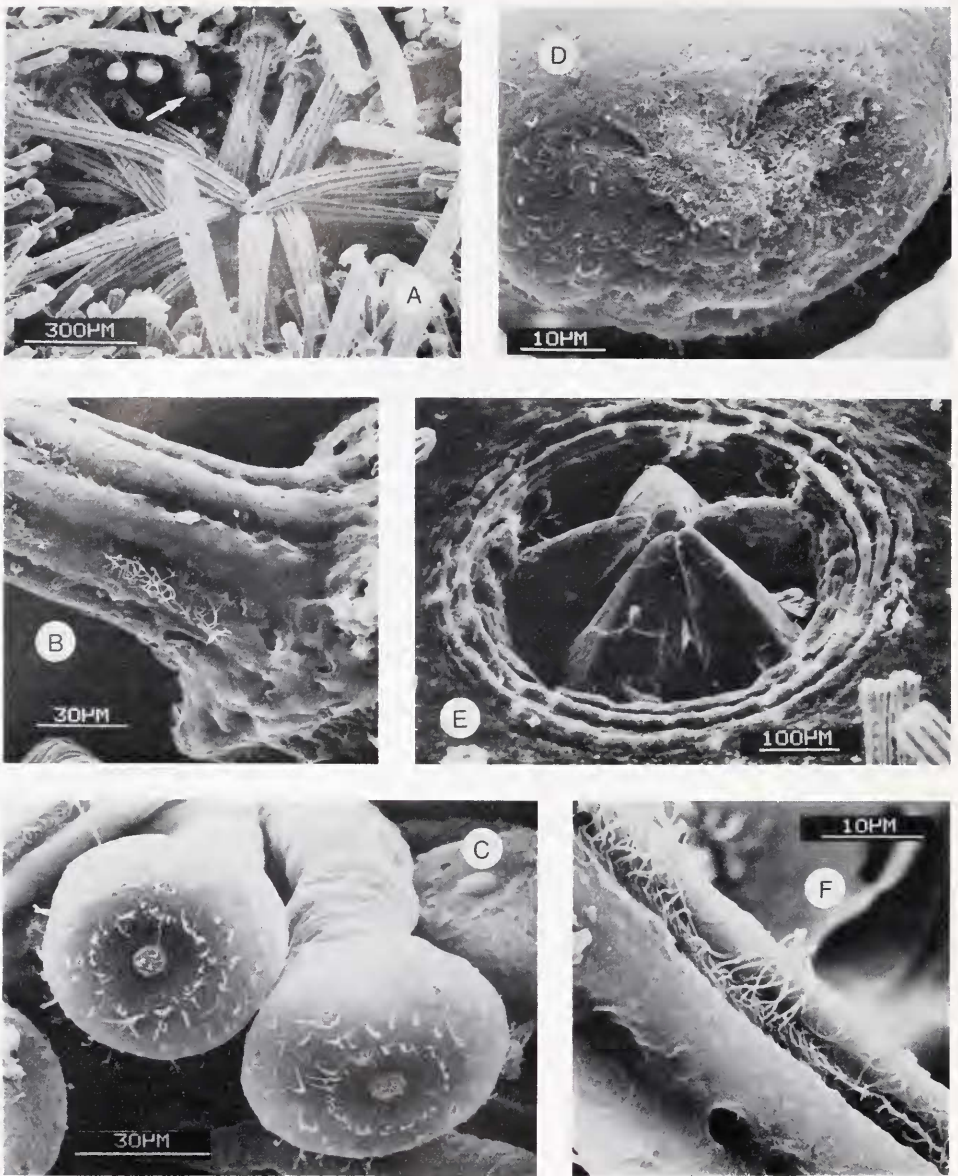
FIGURE 2. Scanning electron micrographs of *Echinocyamus pusillus.* (A) Tiered arrangement of circum-oral spines covering mouth; arrow indicates large, paired buccal podia. (B) Base of primary spine showing short band of cilia. (C) Tips of suckered podia showing cilia surrounding central nipple. (D) Sensory pad at tip of buccal podium, with scattered sensory cilia. (E) Mouth with circum-oral spines removed to show lips and protrusion of lantern teeth. (F) Distal end of miliary spine with band of cilia.

and native mineral particles in proportion to their occurrence in the substrate. Particles travelled towards the mouth area from podium to podium, until they reached the fringing circum-oral spines (Fig. 2A). These spines are arranged in two or three tiers, shorter spines near the mouth, longer ones further away, so that all of their tips can just reach the mouth itself. Five pairs of large buccal podia (Figs. 2A, D), much less

active than suckered podia but nonetheless highly extensible, surround the mouth. Fully elongated, they extend more than half way across the peristome and can readily reach into the mouth. Substrate particles arriving at the mouth region were received by the circum-oral spines and slowly manipulated into the mouth itself. During this process the particles were delicately explored by the buccal podia which collected loose organic material from the surface, or material dislodged by the action of the spines. This material was sometimes passed directly into the mouth by the podia and sometimes by the spines themselves. The greatest bulk of food, however, was obtained by the gnawing and scraping activity of the lantern teeth (Fig. 2E). Substrate particles were held against the teeth and, assisted by the circum-oral spines, they were carefully revolved by the free edge of the peristomial membrane, which functioned as a set of five mobile lips. When the particle had been stripped clean it was finally released and fell away from the mouth.

Anatomy of feeding structures

The tips of the suckered podia bear a ring of sensory cilia surrounding a central nipple (Fig. 2C) with more scattered cilia distributed outside the ring. Inside the ring of cilia there are numerous small secretory cells (10 μm in length) which stain brightly in azan (as noted by Nichols, 1959) and in Milligan's trichrome. Longer, very narrow secretory cells (15–17 μm) on the margin of the disk, outside the ring of cilia, are toluidine blue and PAS positive. These larger cells, which were not described by Nichols (1959), are difficult to detect in *E. pusillus* but are more conspicuous in other clypeasteroids (Mooi, 1983). Both types have external pores from which substances are exuded. These and other aspects of the detailed anatomy of the suckered podia have been treated by Nichols (1959) and Mooi (1983). The buccal podia (Fig. 3) also show features not observed by Nichols (1959). Many short sensory cilia are scattered over the large sensory pad (Figs. 2D, 4A). They are not confined to an outer ring, nor are they especially more numerous around the margin of the pad. The epithelium covering all surfaces of the spines and podia, including the sensory pad of the buccal podia, is densely supplied with microvilli. No cuticle is visible by SEM and the structure reported by Nichols (1959) is most probably the surface layer of microvilli. Around the sensory pad and extending towards its center there are numerous small pores (0.2–0.3 μm) among the microvilli (Figs. 4A, B) as in the suckered podia. Both PAS and triple stained sections show secretory cells wedged into the fibrous material of the sensory pad. Although the miliary spines are alleged to secrete mucus (Ghiold, 1982) we were unable to find any evidence of it. The tips of the miliary spines are covered by smooth, uninterupted epithelium without any pores (Fig. 4C). No secretory pores could be found along the spine shafts. Histological sections show that the lumen of the miliary spines is packed with darkly staining nuclei and granular material, which is quite unlike the secretory cells found in the podia. The peristomial membrane is flexible and allows the lantern teeth to protrude slightly (Fig. 2E). It is thickened into lips (Figs. 5, 6) which grip substrate material during feeding. Histological examination shows a substantial layer of collagenous connective tissue which stains blue with azan and green with Milligan's trichrome. This layer is much more developed than in other clypeasteroids and is covered by epidermis which contains thickened areas of ciliated, secretory tissue, especially near the mouth opening. Secretions from these cells in the lips most likely assist in holding particles during feeding. As in the tips of podia, this thickened epithelium is reinforced by supporting fibers. The lips are operated by two layers of muscle, located on the inner surface of the peristomial membrane (Fig. 6). An outer layer of circumferential fibers act as sphincter muscles
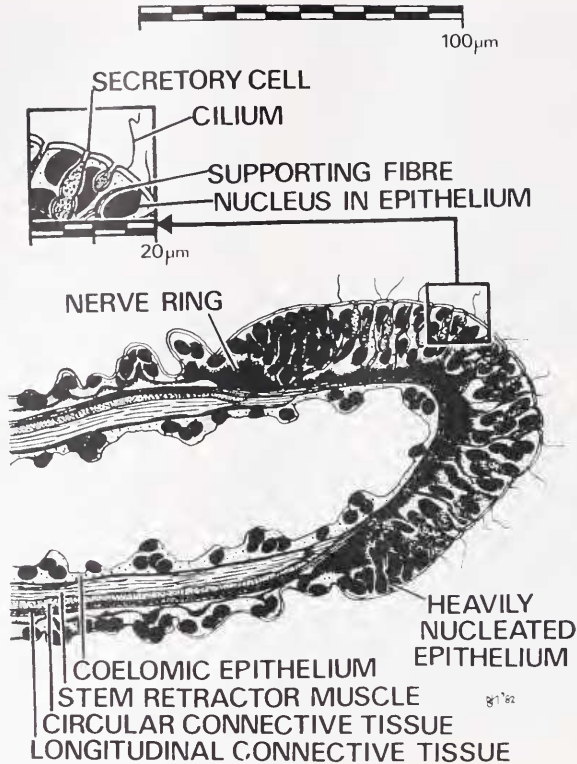
FIGURE 3.   Section of buccal podium. The sensory pad consists of thickened, heavily nucleated epithelium with scattered cilia. Numerous secretory cells, squeezed between the epithelial cells (see inset), have short ducts opening among the epithelial microvilli (also see Figs. 4A, B).

to close the lips. An inner layer of radial muscles attached to the stereom of the peristome opens the lips.

Gut contents and substrate particles

Substrate particles selected by the suckered podia during feeding were often covered with organic material. Under light microscopy much of this appeared to be amorphous, flocculent stuff, but some diatoms and other algae were visible. Washed material prepared for SEM lacked most of the amorphous component but extremely numerous diatoms were found on many particles (Fig. 4D). Both light microscope and SEM examination of the gut contents of *E. pusillus* revealed fragmented and whole diatoms, small pieces of echinoderm spines, sponge spicules, forams, pieces of crustacean cuticle and setae, fragments of multicellular algae, assorted pieces of organic debris, and a few mineral fragments smaller than 0.25 mm. Diatoms made up much the greatest part of the recognizable material in the gut. Those identified included species of *Navicula, Nitzschia, Pinnularia, Pleurosigma, Fragilaria,* and *Cocconeis.* Several unidentified diatoms were also present.

DISCUSSION

The occurrence of *Echinocyamus pusillus* in shelly gravel or sand has been well documented (Mortensen, 1948; Nichols, 1959; Ghiold, 1982). Our observations in
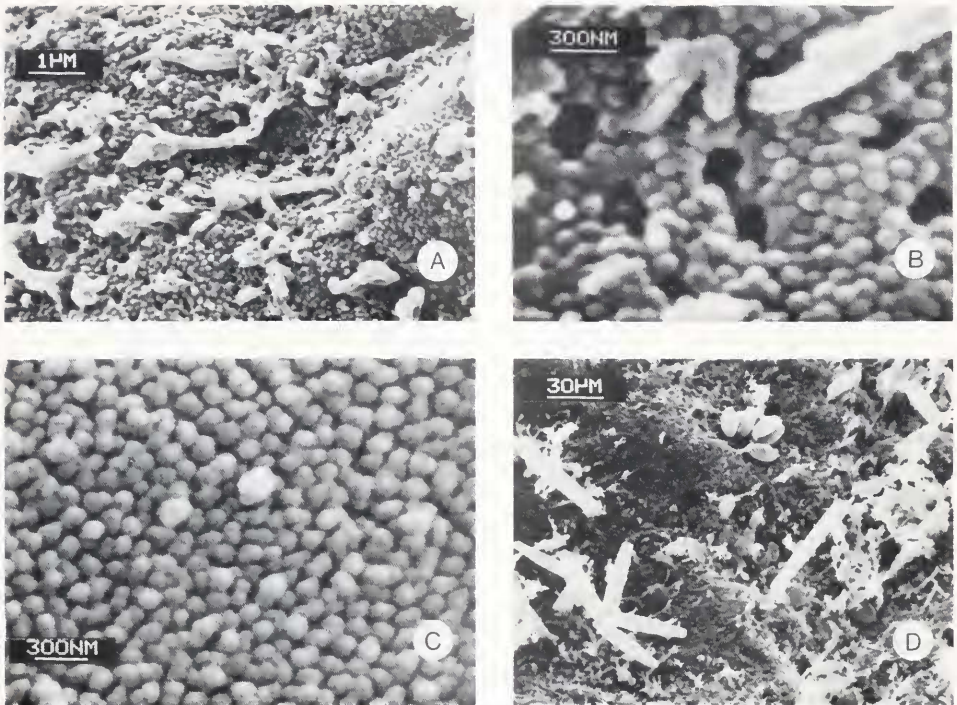
FIGURE 4. Scanning electron micrographs of *Echinocyamus pusillus*. (A) Cilia, microvilli, and secretory pores in sensory pad of buccal podium. (B) Microvilli and secretory pores (as in Fig. 4A). (C) Epithelial microvilli of miliary spine: no secretory pores were found anywhere on the spines. (D) Diatoms attached in shallow hollows of sand grain. Numerous mucilaginous threads mark earlier sites of attachment.

the Firth of Lorne suggest that the species occurs most commonly on substrates exposed to extensive wave and tidal current activity. These substrates may be disturbed and turned over frequently by current action and are, presumably, relatively well aerated. *Echinocyamus pusillus* was scarce or absent in fine, muddy sediments in sheltered areas (Fig. 1 and Table III) although Wolff (1968) was of the opinion that it might occur on such substrates. Other investigators (cited above) have emphasized the shell component of the substrate. The significance of this, if any, is difficult to determine. We have found *E. pusillus* to be abundant in gravelly substrates virtually free of shell debris and in substrates where shell rubble constitutes 90% or more of the particles (Table III). It seems likely that a wide range of particle sizes, including large pebbles with finer material between, and strong current exposure are the critical requirements. In the laboratory, *E. pusillus* ceased feeding when water flow, and hence oxygenation of the substrate, was low. In such active environments, shell debris may accumulate or even originate more readily from neighboring mollusc populations. We saw no evidence that the shell component was used preferentially by *E. pusillus* nor that the resident flora was greater than that on abiogenic particles. This observation is further supported by the fact that substrate organic contents were not related to the shell:mineral particle ratios. In fact, the most shelly substrates included both the lowest and highest percentages of organic material. SEM examination of substrate particles shows numerous diatoms, including many of those found in the gut of *E. pusillus*. Those shown in the SEM micrograph (Fig. 4D), are mostly attached in hollows of the grain surface, as noted by Meadows and Anderson (1968). The mi-
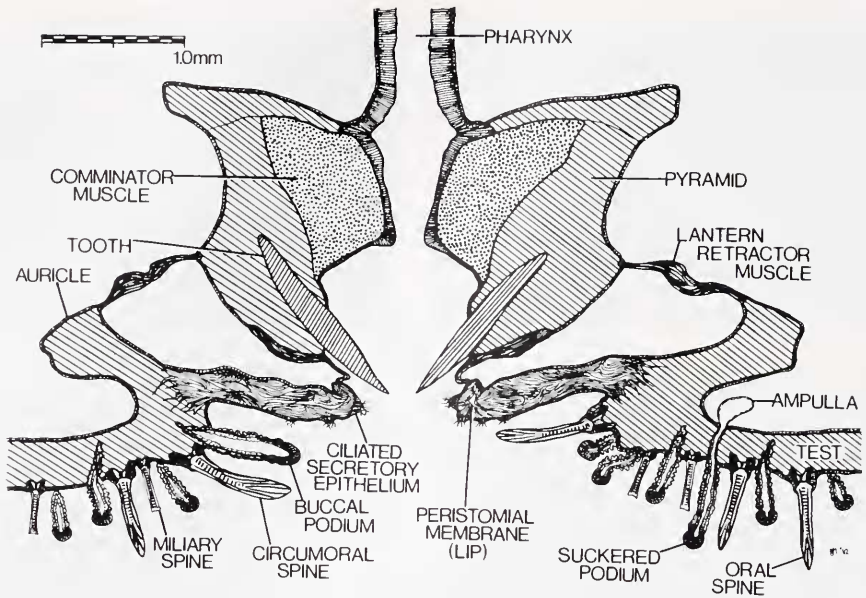
FIGURE 5. Cross section through mouth of *Echinocyamus pusillus* showing thickened peristomial membrane. The free margin of the membrane serves as a set of mobile lips which hold substrate particles in place while the lantern teeth strip away diatoms.

crograph also shows remnants of many more mucilaginous threads where diatoms were formerly attached.

The feeding mechanism of *E. pusillus* is markedly atypical of clypeasteroids, as Nichols (1959) correctly surmised. The use of the suckered podia to collect and transport food-bearing particles and, most especially, the use of the lantern teeth, is more characteristic of regular echinoids than any other group. The action of the lips at the margin of the peristomial membrane was quite unexpected and is unlike any mechanism previously described in feeding of clypeasteroids, such as sand dollars. It should, however, be noted here that sand dollars make extensive use of their accessory podia in drawing particles onto the sieving mechanism of the aboral surface (Goodbody, 1960; Bell and Frey, 1969; Mooi and Telford, 1982). Furthermore, *Clypeaster rosaceus*, another aberrant clypeasteroid, uses both the suckered podia and lantern teeth in a similar fashion.

Contrary to the opinion of Nichols (1959), the buccal podia do not seem to be solely sensory in function. Nichols did not observe secretory cells in these podia but in our sections they were present, in and around the sensory pad (Fig. 3). The pores seen among the microvilli (Fig. 4A, B) correspond in position with these cells and could be secretory outlets. These pores were never visible in areas lacking secretory cells. In addition to a major sensory function, the buccal podia are used also in collecting and transferring some of the food into the mouth. This use invites comparison with the feeding of spatangoids but the functional similarity is superficial, resting mostly on secretion of sticky substances. The simple paired buccal podia of fibulariids in no way approach the sophistication of the highly modified spatangoid feeding organs.

Ghiold (1982) reported the presence of large mucus secreting pores at the tips of miliary spines. In this study, histology did not show any evidence of secretory material

ESOPHAGEAL EPIDERMIS

CIRCUMFERENTIAL⌐
RADIAL⌐MUSCLE
LAYERS

CILIUM

COLLAGENOUS
CONNECTIVE TISSUE

SECRETORY
CELL
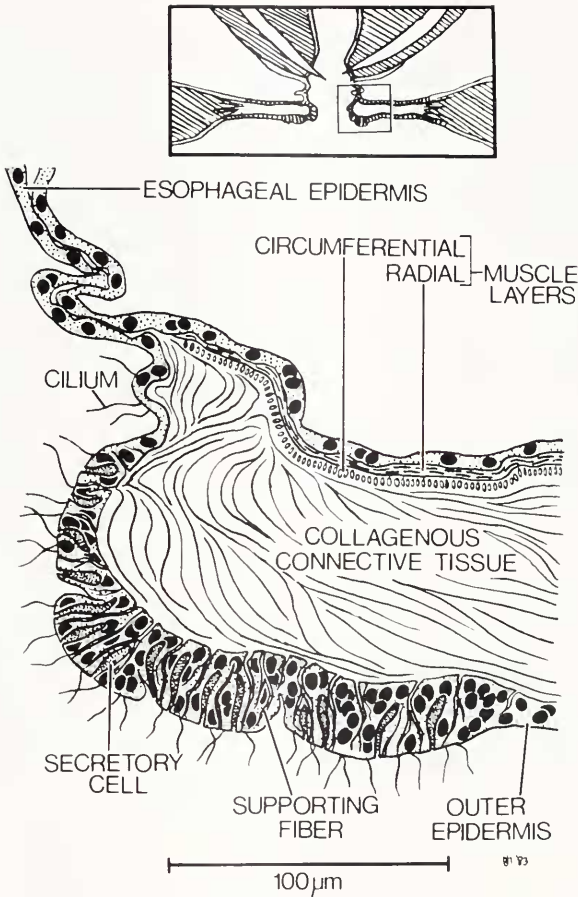
SUPPORTING
FIBER

OUTER
EPIDERMIS

100 μm

FIGURE 6. Section of edge of peristomial membrane (lip). The surface of the lip region is covered by thick secretory epithelium with scattered cilia. The lips are retracted by an inner layer of radial muscle fibers and closed by circumferential fibers.

in these spines. The lumena are filled with darkly staining nuclei and granules which do not react like secretory material with PAS or toluidine blue. Furthermore, SEM showed the total absence of pores in miliary spine epithelium (Fig. 4C). The large, terminal pores shown by Ghiold (1982) are undoubtedly artefacts due to poor specimen preparation: air-dried material is unsuitable for cellular details, such as microvilli, secretory pores, or cilia. The relatively large holes and depressions along the spine shafts (Figs. 2B, F) correspond with openings in the underlying stereom. The absence of secretory cells or granules within the spines, indicates that these openings, which might be artefacts, are not secretory pores.

Sand dollars such as *Leodia* and *Mellita* are thought to use the primary and miliary spines as a two-tiered sieve mechanism (Goodbody, 1960; Bell and Frey, 1969; Seilacher, 1979; Lane and Lawrence, 1982) which dislodges diatoms and organic debris from substrate particles. This material is then collected by ciliary currents and perhaps mucus secretion, moved to the mouth along well-defined food grooves, and there ingested. No such mechanism exists in *E. pusillus*. It is equipped with some of

the requisite structures but lacks others. There is a very clear differentiation between primary and miliary spines and the distribution of cilia on them is almost identical to that of *Echinarachnius parma* (Mooi and Telford, 1982). Ghiold (1982) has hypothesized that early clypeasteroids exploited surface cleansing currents as a new feeding system and that spine differentiation in *Echinocyamus* represents pre-adaptation in an early stage of the evolutionary development of this new mechanism. He offered no explanation of the possible adaptive significance of spine differentiation during this "pre-adaptational" stage. It is curious that the miliary spines of *E. pusillus* are more sharply differentiated and have more elaborate crowns than those of almost any other clypeasteroid. Others with highly differentiated miliary spines, although of somewhat different form, include the rotulids and mellitids, which are generally conceded to be advanced forms. Thus, according to this feature, *E. pusillus* could be regarded as advanced, not primitive. Departure from the characteristic mode of food transport in the clypeasteroids may also be considered as a secondary, specialized feature. The absence of any vestige of the food grooves or of a podial arrangement reminiscent of them, raises some interesting questions about the possible point of evolutionary divergence of the Fibulariidae. As remarked earlier, the family is generally placed close to the Laganidae, which have distinct but short food grooves, and the Rotulidae in which the grooves are much branched. Other clypeasteroids which have developed secondary feeding mechanisms, such as *Dendraster excentricus* (Timko, 1976; O'Neill, 1978), have retained clear food grooves. This species, of course, readily feeds in the conventional mode as well as in the upright posture.

In summary, we tend to agree with the early opinion of Clark (1914) that *Echinocyamus pusillus* is a specialized, not a primitive species. Spine differentiation and ciliation are characteristics shared with all clypeasteroids, which makes it unlikely that *Echinocyamus* could in any sense represent an ancestral form of the true sand dollars. Their small size is most probably an adaptation to existence in pockets of sediment between frequently moving pebbles or stones, on substrates worked by currents. The rocking sieve mechanism described for some species, appears to work best with the relatively fine particles found in well-sorted substrates in which sand dollars most commonly occur. The small surface area of the specialized fibulariids provides insufficient spines to make an effective sieve. They rely, instead, on the collection of individual particles from which food material can be stripped by the lantern teeth.

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